

# SWARMING IN A BALLOON-CARRYING EMPIDID (EMPIDIDAE: *HILARA*)<sup>1</sup>

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## INTRODUCTION

Swarms are perhaps the most spectacular of insect mating aggregations. Usually groups of males fly at particular stations or markers where females come to locate mates (Sullivan 1981). Swarming behavior is particularly common in Diptera, the flies. In one family, the Empididae, it is especially well known because swarming males often carry gifts of prey which are presented to females during copulation (i.e. nuptial feeding, Downes 1969). The gift-giving has become ritualized in some empidids and "balloons" made of glandular secretions produced by males are transferred to females at coupling (Kessel 1955). Balloon flies are found among three genera of empidids (*Empimorpha*, *Empis*, *Hilara*).

Though a large and diverse group of flies, few species of empidids have been extensively studied in the field (Alcock 1973, Chvala 1976). In North America only five balloon-carrying species have been studied (Kessel 1959) and all occur in western United States and Canada. This report is the most extensive of the field studies of the swarming and mating behavior of a single species of balloon fly and is the first detailed study of a balloon fly from the eastern U.S.

## MATERIALS AND METHODS

The study site was the edge of a 50 × 100 m wooded area adjacent to cultivated fields at Green Acres Farm, Dept. of Agronomy, University of Florida (NE 1/4, sec. 27, tp. R18E, T9S). Adult season in Gainesville lasts about 2 weeks during late March or early April. I

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<sup>1</sup>Dr. Paul H. Arnaud, Jr. has examined specimens and determined this to be a new species of balloon fly. Voucher specimens have been deposited at the California Academy of Sciences, San Francisco and the Florida State Collection of Arthropods, Gainesville.

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found males swarming in early April 1981, and specific observations were made during the three following springs. I was at the study site each evening 30 min. prior to daily swarming.

*Male activity.* Male swarming periods were monitored on 12 days (1982  $n = 9$ , 1983  $n = 3$ ). The start of swarming was noted when the first male was seen constructing a balloon at a swarming station and three more males were seen during the next minute. At the start of activity, light intensity was indexed by estimating the percent (nearest 10%) of the sky occluded by clouds. Temperature and wind speed at a height of 1 m were also taken. Activity period stopped when no males were found at swarming stations monitored that evening. All swarms of a given evening broke up within a 3 min. period.

*Swarm station, height, size.* Each swarming station was marked with a numbered wooden stake put into the ground below the swarm. Height of swarms was measured to the nearest .1 m with a 2.5 m pole marked at .1 m intervals. Measurement was taken from ground level beneath swarms to swarm center.

White balloons carried by males made them conspicuous and the number of males in a swarm (size of swarm) was estimated by counting balloons. Since females and possibly some males do not carry balloons, only displaying males were counted. Because of movement by males in swarms and difficulty in counting balloons, swarms with more than 10 males were estimated to the nearest 5 males.

*Mating behavior.* During swarming considerable effort was made to locate and watch pairs as they coupled and mated. As some pairs formed in the swarm they were collected. Uncoupled members of the swarm were also captured. The sizes of females, coupled males and uncoupled males were measured to investigate whether or not large males were more likely to mate with females. Size was determined by measuring with a ocular micrometer the lengths of a wing and hind femur of each individual.

## RESULTS

Both sexes were found on leaves near swarming stations 15–30 min. prior to swarming activity. During this time males flew from leaf to leaf and walked along the leaf margins from the base to tip and then back again, possibly searching for females.

At about sunset swarms formed beneath branches of broadleaf trees (*Quercus*, *Prunus*, *Myrica*). Particular branches (stations) were used from 1 to 8 nights during a season and swarming occurred at some stations all four years (1981–1984). Average height of swarms was 1.7 m (range 0.5–4.5 m, Fig. 1). Most swarms contained fewer than 5 males but some swarms had over 20 males in a space of less than  $25 \times 25 \times 25$  cm (Fig. 2).

Swarming started about sunset and continued for 20 minutes (Fig. 3A). High winds (gusts  $> 10$  kmph) often delayed or halted swarming and swarms never formed at temperatures below  $13^{\circ}\text{C}$ , even though individuals were seen on leaves prior to the activity period. The starting and stopping of swarming was negatively correlated with cloud cover ( $r = -.81, -.90$ , respectively;  $p < .05$ ). That is, when greater percent of the sky was covered by clouds swarming started and ended earlier in the evening (Fig. 3B).

Males in the swarms carried a 2–3 mm spherical, white, silken balloon below them while they flew. The balloons were hollow, did not contain prey, and were constructed with silk from tarsal glands while in flight. Male movement in swarms was easily followed by watching the white balloons against a background of foliage or males silhouetted against the sky. Males generally flew side-to-side in swarms and often males (balloons) collided. Twice a male was

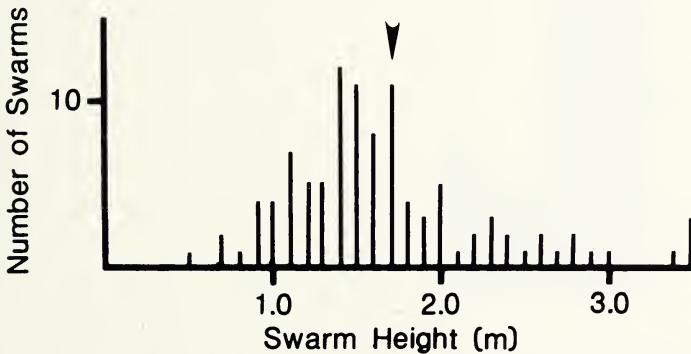


Figure 1. Frequency distribution of height of *Hilara* n. sp. swarms ( $n = 103$ , during spring 1982 & 83) at Green Acres Farm, Dept. of Agronomy, Gainesville, Fla. Two swarms at heights of 3.7 and 4.5 m are shown at 3.5 m. Arrow represents mean height.

seen flying from a swarm with his balloon trailing by a silken thread. Upon landing on nearby vegetation the balloons were lost and never retrieved. These balloons were probably dislodged during a collision with another male in the swarm. It is not known whether these two males constructed new balloons and returned to a swarm that evening. Some individuals left a group, joined another more than 1 m away, and sometimes returned to their initial swarm, but in general males remained at the same station for the entire swarming period.

Females perched on vegetation near swarms and flew into swarms where coupling occurred. Pairs were easily distinguished from the more erratic flight of uncoupled males. Mating (coupling) occurred during the last 8 min of the activity period ( $n = 22$  pairs, range 1–19 min.). When couples were captured, males were mounted atop

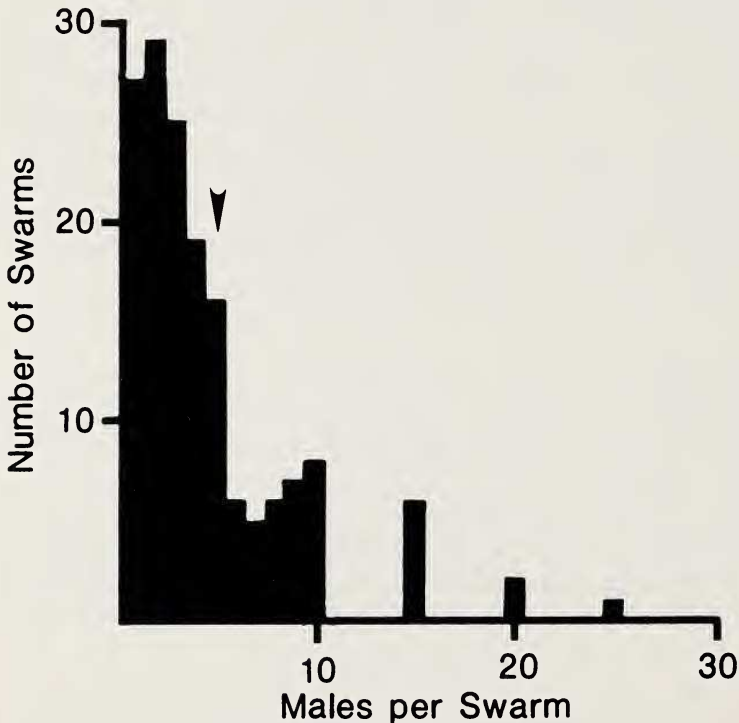


Figure 2. Distribution of swarm size as measured by counting the number of balloons in 156 *Hilara* swarms (spring 1982 & 83). Swarms with more than 10 males were estimated to the nearest 5 males. Arrow shows mean size of swarms.

females that now held but did not eat the balloons. Males held females by the thorax with their enlarged forelegs. Pairs kept in vials remained coupled for 2–6 min.

Some couples left swarms and hovered at the edge of the woods. Once swarming ceased, more pairs were found flying near the wood's edge. Due to failing light pairs could not be followed for more than a couple of minutes during which time pairs never separated or landed.

Females are significantly smaller than males in both wing length and hind femur length. However, males that were captured while mating did not differ significantly in femur length but had signifi-

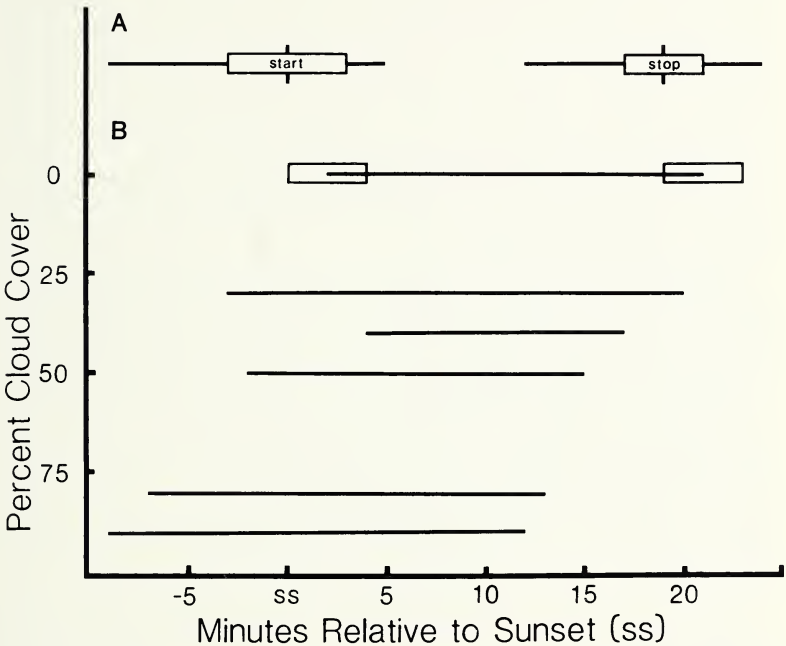


Figure 3. A. Average starting and stopping times of swarming for 12 nights (1982 and 1983). Vertical lines are means, horizontal lines are ranges, and bars represent 95% confidence intervals of means. Average duration of swarming is time between average start and stop. B. Daily duration of swarming for 12 nights in 3A relative to cloud cover at the beginning of swarming. Duration shown for clear days (0% cloud cover) is the average for 7 nights. Note the correlation between cloud cover and start and stop of swarming ( $r = -.81, -.90$ , respectively).

cantly shorter wing lengths than uncoupled males captured in swarms (Table 1).

#### DISCUSSION

Kessel (1955), expanding on Hamm's (in Poulton 1913) and Melander's (1940) classification, recognized eight stages in the evolutionary sequence of empidid mating behaviors. The eighth and final stage is represented by balloon-carrying species in which males swarm and the balloon alone has become the stimulus for courtship and mating. *Hilara* n. sp. thus is a representative of this stage.

Two of the other five North American balloon flies that have been studied are *Hilara* species. *Hilara wheeleri* is similar to *Hilara* n. sp. in that males swarm near broadleaf trees at heights less than 2 m, balloons are made of silk from tarsal glands. However, dipteran prey are always encased in the walls of the balloon (i.e. stage 5 of Kessel's sequence). *Hilara granditarsis* swarms at heights more than 3 m high in the branches of coniferous trees and males carry frothy balloons that contain no prey (stage 8). *H. sartor*, a European species, also swarm high in the branches of conifers and have frothy balloons without prey (stage 8).

Congregating on leaves before swarming may occur because both males and females respond to the same conspicuous landmark. One hypothesis on the evolution of swarming behavior is that going to such markers has been an efficient mechanism for unmated females to locate mates (Sullivan 1981). Selection then acts on both males and females to respond to these conspicuous landmarks. Though male *Hilara* appeared to search for females they did not try to court or mate with females on nearby leaves. Once males reach an area using long range visual cues they should try to locate specific swarm-

Table 1. Hind femur and wing length (mm) of *Hilara* females, coupled and uncoupled males.\*

	n	femur length $\bar{x} \pm \text{S.D.}$	wing length $\bar{x} \pm \text{S.D.}$
females	8	1.06 $\pm$ .05 <sup>A</sup>	3.2 $\pm$ .1 <sup>A</sup>
coupled males	10	1.15 $\pm$ .06 <sup>B</sup>	3.4 $\pm$ .1 <sup>B</sup>
uncoupled males	22	1.20 $\pm$ .06 <sup>B</sup>	3.5 $\pm$ .1 <sup>C</sup>

\*Means in a column with different letters are significantly different ( $p < .05$ ).



ing sites that will be most profitable with respect to female-to-competitor ratio.

The time of swarming is restricted to a 20-minute period at dusk (Fig. 3). Crepuscular swarming is common in insects presumably because climatic factors, especially wind, are more favorable for swarming (Sullivan 1981). For balloon flies the change in light quality and quantity, particularly at sunset, may influence when the balloon would be most efficient in attracting females. Light does influence the timing of *Hilara* swarms since their activity begins and ends earlier in the evening on cloudy days (Fig. 3).

Males are expected to display when reproductive benefits are greater than alternative behaviors. That is males should swarm when females are most available and attractive to mates. When their availability is confined to brief periods females may "force" males to display synchronously. This benefits females since when large numbers of males display together females have a greater choice from potential mates. From this positive-feedback mechanism evolves the spree, a temporal analog of a lek (see Walker 1983).

Swarms are restricted in space as well as time and may therefore be compared to a lek where males display and females come to mate with males. Most often only a few males in the leks do all or most of the mating and females receive nothing more than sperm from their mates (Bradbury 1981). That *Hilara* females remain on vegetation during swarming and do not, until late in the swarming period, enter the swarm and couple with a male suggests that they may be evaluating males in swarms. The cue used in this evaluation remains in doubt. Perhaps the balloon is an effective means by which females can judge male vigor on the basis of flight patterns made more noticeable by the conspicuous balloon. Or once coupled a female might "analyze" the composition of the balloon as an indicator of a male's ability to accrue certain resources (Thornhill and Alcock 1983). This would be very important in species that presented prey as nuptial gifts.

That males are larger than females (Table 1), unusual in insects, points to selection for large males. Males that join swarms must compete for a limited number of females and, since males collide with others and mating takes place in the swarm, large males might have an advantage. However, it was found that coupled males had smaller wing lengths than those that were uncoupled (Table 1). That

coupled males did not differ significantly in femur length indicates that coupled males have higher wing loading (wing area relative to body size) than uncoupled males. This wing loading difference may be important to a male's ability to maneuver in the swarm.

But why should mating pairs remain in the swarm? Males risk losing females in fights with other larger males in the swarm and females might be injured in such flights. An advantage a male might have would occur if mating durations are relatively short compared to the time remaining in the swarming period. Males then might profit by remaining in the swarm and continuing to advertise for other females. If a male has been selected by a female that evening he "knows" that he has outcompeted the other males in the same swarm. Provided females will mate with males that have already mated that evening, males will gain by remaining in the swarm. However, pairs were found hovering near the edge of the woods and durations of mating last until after swarming has ceased. Another alternative is males may remain in the swarm to exercise some choice over females that enter. If female size is an indication of her reproductive output then males may be waiting to see if a larger female enters the swarm. A male would gain reproductively by mating with a larger more fecund female. A female, on the other hand, might exercise her choice and fly back into the swarm if she is coupled to an unwanted male and force the male to prove his competitive ability.

#### SUMMARY

Mating swarms of *Hilara* sp. are made conspicuous by white, silken balloons carried by males. Groups of 1-25 males swarm beneath branches of broadleaf trees at a modal height of 1.4 m (range 0.5-4.5 m). Male activity periods begin about sunset and continue for 20 minutes with the beginning and ending of swarming correlated with light intensity. Females fly into swarms where coupling occurs. Unlike most other swarming Diptera, *Hilara* sp. pairs remain in the swarm while mating. Males are larger than females, though coupled males were significantly smaller (wing length) than other males in the swarm.



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